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Reciprocal human-natural system feedback loops within the invasion process

James S. Sinclair[1], Jeffrey A. Brown[2], Julie L. Lockwood[3]

1 *Aquatic Ecology Laboratory, Ohio State University, Ohio, USA* **2** *Julie Ann Wrigley Global Institute of Sustainability, Arizona State University, Arizona, USA* **3** *Ecology, Evolution and Natural Resources, Rutgers University, New Jersey, USA*

Corresponding author: James S. Sinclair (sinclair.130@osu.edu)

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Abstract

Biological invasions are inextricably linked to how people collect, move, interact with and perceive non-native species. However, invasion frameworks generally do not consider reciprocal interactions between non-native species and people. Non-native species can shape human actions via beneficial or detrimental ecological and socioeconomic effects and people, in turn, shape invasions through their movements, behaviour and how they respond to the collection, transport, introduction and spread of non-natives. The feedbacks that stem from this 'coupled human and natural system' (CHANS) could therefore play a key role in mitigating (i.e. negative feedback loops) or exacerbating (i.e. positive feedback loops) ongoing and future invasions. We posit that the invasion process could be subdivided into three CHANS that span from the source region from which non-natives originate to the recipient region in which they establish and spread. We also provide specific examples of feedback loops that occur within each CHANS that have either reduced or facilitated new introductions and spread of established non-native species. In so doing, we add to exisiting invasion frameworks to generate new hypotheses about human-based drivers of biological invasions and further efforts to determine how ecological outcomes feed back into human actions.

Keywords

coupled human and natural systems, coupled social-ecological systems, feedback loop, invasive, negative feedback, non-native, positive feedback

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Introduction

Humans are the principal drivers of biological invasions (see the Glossary in Box 1 for the definition of 'invasive'), evinced by the much higher rate of invasions in the modern era (Ricciardi 2007) and the wealth of literature detailing how people aid the establishment and spread of non-native species (e.g. Suarez et al. 2001; Wilson et al. 2009; Capinha et al. 2015). The invasion process could, therefore, be considered as a 'coupled human and natural system' (CHANS; defined by Liu et al. 2007) because natural components (i.e. non-native species and the environments or communities they impact) interact with and are affected by human behaviour and socioeconomic activity. However, none of the major hypotheses in invasion ecology (summarised by Catford et al. 2009) and few conceptual frameworks of the invasion process (e.g. Richardson et al. 2000; Colautti et al. 2006; Blackburn et al. 2011) explicitly considers reciprocal feedbacks (hereafter termed 'feedback loops') between humans and non-native species

Box 1. Glossary of terms.

Impact: Observable effects of non-native species, which can include ecological, economic and human health effects and changes in the provisioning of ecosystem services

Intentional: The intentional human-mediated transport and introduction of non-natives, such as for horticulture, the pet trade or biocontrol

Invasive: A non-native species with demonstrable impacts

Negative feedback loop: A human-natural feedback that continually stabilises or reduces ongoing or future invasions (also known as a 'balancing' feedback loop)

Non-native: Species moved outside their native range by human actions

Positive feedback loop: A human-natural feedback that continually increases ongoing or future invasions (also known as 'exacerbating' or 'reinforcing' feedback loops)

Recipient region: The specific location or region into which non-natives are introduced

Source region: The specific location or region from which a non-native originates

Unintentional: Non-natives whose human-mediated transport and introduction is entirely accidental, such as via hitchhiking on vehicles or through constructed corridors

(but see Lodge et al. 2009; Howard 2019). Feedback loops are a distinguishing feature of CHANS because they are indicative of two, fully linked systems in which one system both drives and responds to changes in the other. These types of human-ecological feedback loops often produce unexpected interactive effects, such as sudden threshold shifts or lagged responses (Parker et al. 2008; Kramer et al. 2017). If these feedback loops exist for biological invasions, then identifying and incorporating them within invasion frameworks is essential to understanding how people can slow invasion rates, reduce negative invader impacts or accelerate stages of the invasion process.

We posit that three CHANS feedback loops can manifest within different stages of the invasion process, spanning from the initial source region where non-native species originate to the recipient region where non-natives establish and spread (Fig. 1). Each of these CHANS can produce 'negative' feedback loops that slow the rate of new species invasions over time and 'positive' feedback loops that accelerate invasion rates or exacerbate the impacts of previously-established invasive species (see examples in Fig. 2). Explicitly recognising the potential for multiple socioecological feedback loops within the invasion process elevates the relevance of existing published evidence that humans play a strong role in invasions. Additionally, recognising CHANS within the invasion process shifts the role of humans away from being simply vectors or unidirectional interactors with ecosystems that prime the way for invasions (Gurevitch and Padilla 2004) to one where people and non-native species are continually experiencing reciprocal feedback interactions in ways that can further control, sustain or even magnify invasion rates.

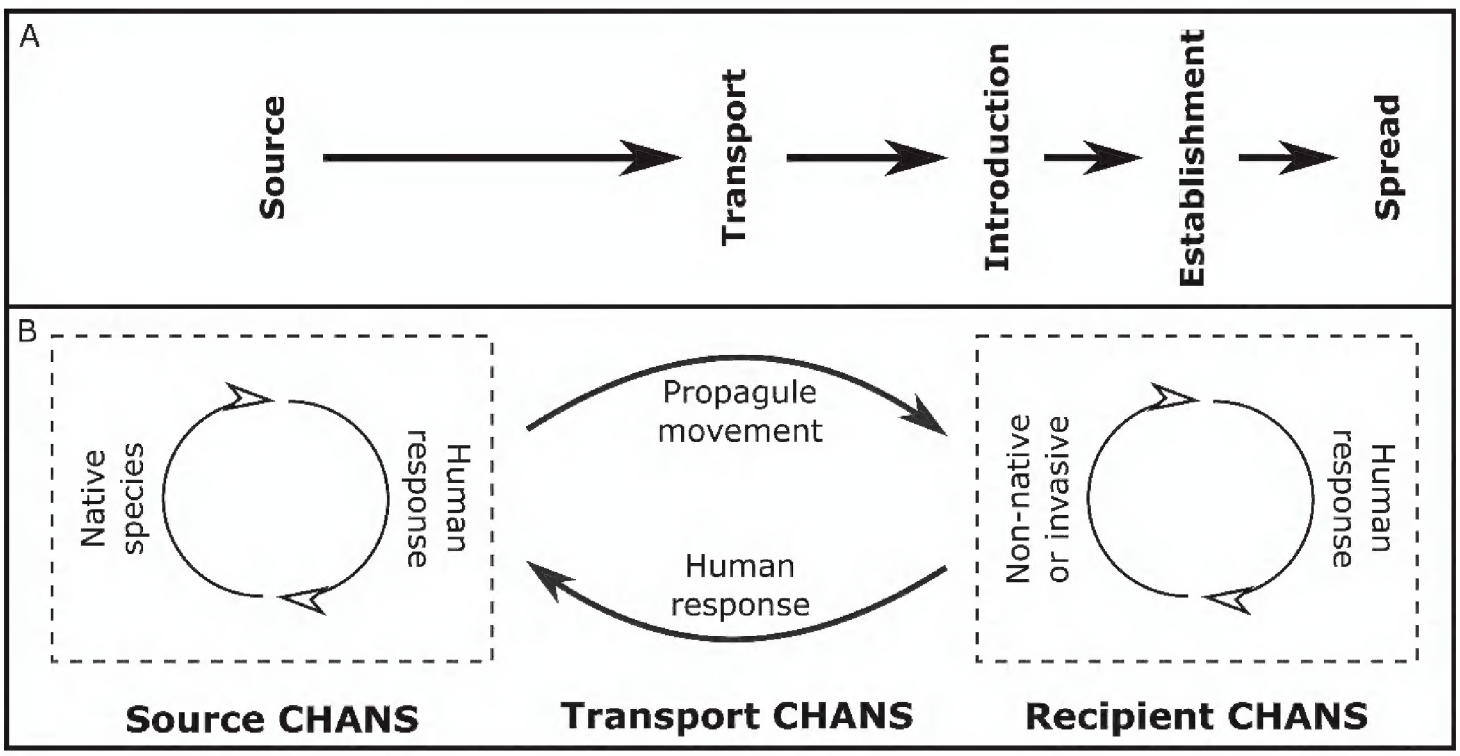


Figure 1. Comparison of (**A**) the different stages of the invasion process (based on Colautti et al. 2006) to (**B**) the three, linked coupled human-natural systems (CHANS) that potentially overlap these stages. The 'Source' CHANS encompassess the response of people in the region from which non-natives originate (i.e. the human system) to changes in and the collection of their own native biodiversity (i.e. the natural system). The 'Recipient' CHANS captures interactions between people and the introduction, establishment and spread of non-natives.The 'Transport' CHANS links the response of people to non-natives in the recipient region to the ongoing and future transport of organisms from the source region.

The first of our three CHANS (the 'source' coupling; Fig. 1A) acknowledges that there are human-natural feedback loops entirely localised within the region from which non-native species are sourced. Source region feedback loops can determine which and how many organisms are collected and transported to a new location (the 'recipient' region). Here, the CHANS is driven by how people in the source region perceive and respond to their local biodiversity, particularly in terms of the availability of species to exploit in trade. This feedback loop also recognises that local environmental or trade regulations can profoundly influence the quantity and diversity of species that enter the invasion process. These regulations may either prohibit the intentional transport of potentially invasive species or limit activities that tend to unintentionally transport individuals of species that may be invasive.

The second feedback loop (the 'transport' coupling; Fig. 2) encompasses interactions between source and recipient regions resulting from the transport of non-native species. Introduced non-native species can influence the ecology, culture, policy, economics or human health of the recipient region. These effects can then feed back to the source

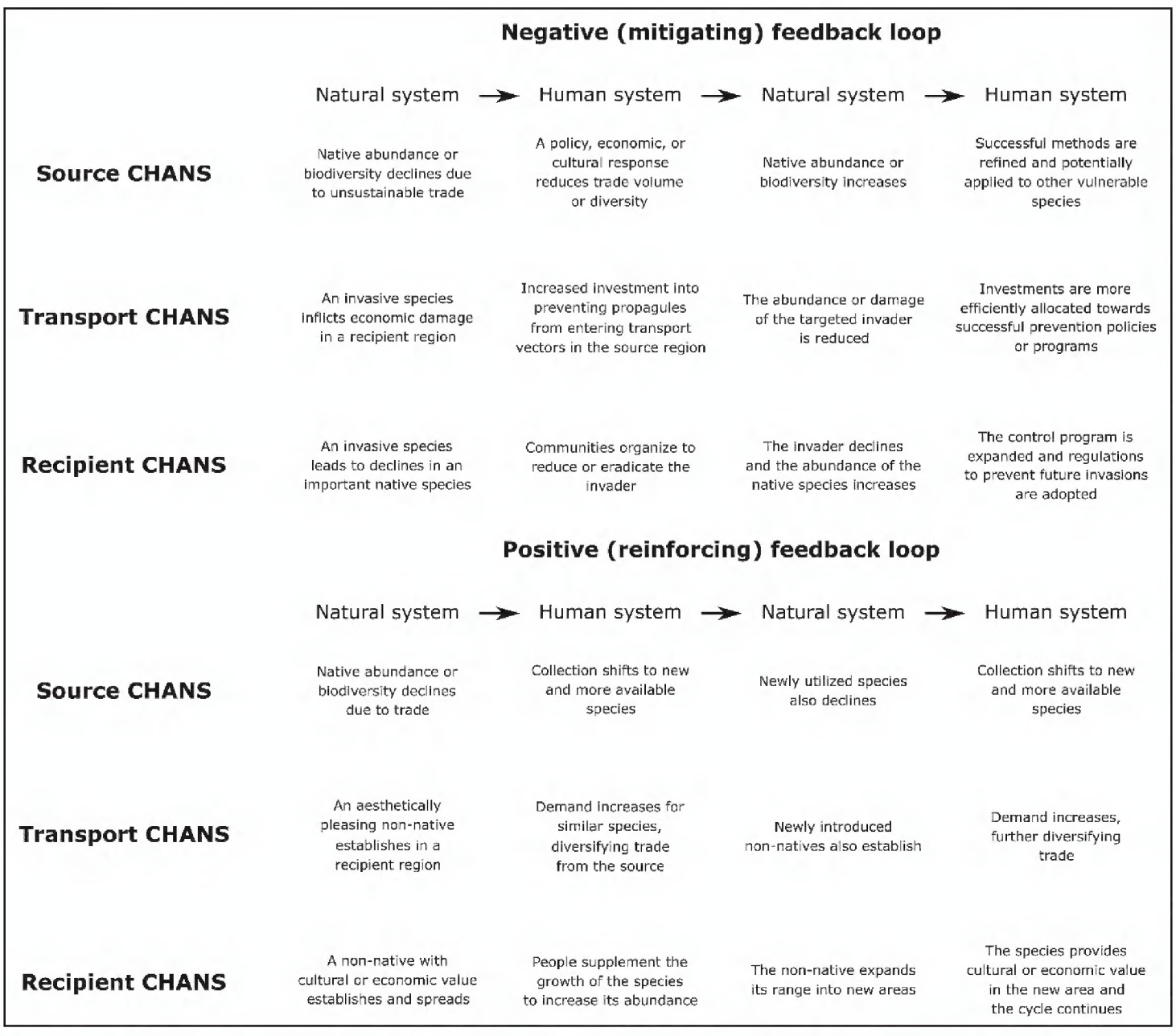

Negative (mitigating) feedback loop
Natural system → Human system → Natural system → Human system
Source CHANS
Native abundance or biodiversity declines due to unsustainable trade
A policy, economic, or cultural response reduces trade volume or diversity
Native abundance or biodiversity increases
Successful methods are refined and potentially applied to other vulnerable species
Transport CHANS
An invasive species inflicts economic damage in a recipient region
Increased investment into preventing propagules from entering transport vectors in the source region
The abundance or damage of the targeted invader is reduced
Investments are more efficiently allocated towards successful prevention policies or programs
Recipient CHANS
An invasive species leads to declines in an important native species
Communities organize to reduce or eradicate the invader
The invader declines and the abundance of the native species increases
The control program is expanded and regulations to prevent future invasions are adopted
Positive (reinforcing) feedback loop
Natural system → Human system → Natural system → Human system
Source CHANS
Native abundance or biodiversity declines due to trade
Collection shifts to new and more available species
Newly utilized species also declines
Collection shifts to new and more available species
Transport CHANS
An aesthetically pleasing non-native establishes in a recipient region
Demand increases for similar species, diversifying trade from the source
Newly introduced non-natives also establish
Demand increases, further diversifying trade
Recipient CHANS
A non-native with cultural or economic value establishes and spreads
People supplement the growth of the species to increase its abundance
The non-native expands its range into new areas
The species provides cultural or economic value in the new area and the cycle continues

Figure 2. Examples of potential negative and positive feedback loops. Negative feedback loops can mitigate or balance invasions, whereas positive feedback loops can reinforce or exacerbate invasions. Examples are presented for each of the three proposed CHANS (source, transport, and recipient; Fig. 1) involved in the invasion process and are discussed further in the text.

region, such as through new prevention policies or shifting consumer demand. The transport feedback loop can span global scales, driven by inter-country travel and trade, but can also include local-scale interactions within a single region, provided propagules are being moved outside their native range (Faulkner et al. 2020; Pergl et al. 2020).

The final CHANS (the 'recipient' coupling; Fig. 2) encompasses local-scale feedbacks in the recipient region between humans and the effects of established non-native or spreading invasive species. This CHANS emphasises that how people respond to non-native populations and associated impacts in the recipient region is driven by local culture, demographics and economics, as well as the traits of the non-native species themselves. The response of local people can be a key driver for mitigating or further exacerbating potential new introductions, as well as promoting or preventing the continued spread of already-established non-native species.

In what follows, we highlight literature that supports key aspects of these three couplings and outline examples that show how human-nature linkages at each of these invasion stages can create both negative and positive feedback loops.

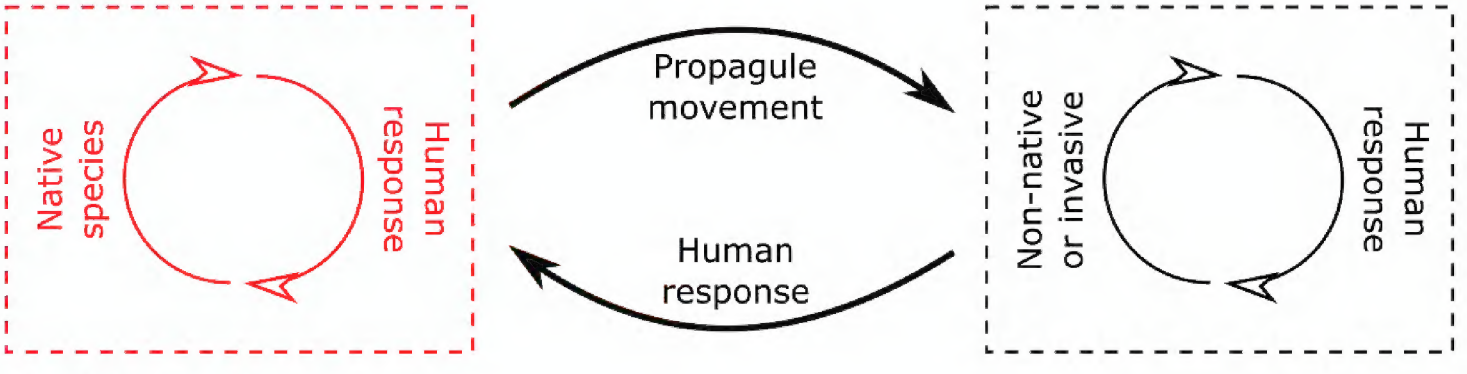
Source coupling

Drivers of source feedback loops

Invasion feedback loops that originate from the source coupling are driven by how people in the source region (i.e. the human system) respond to changes in that region's native species (i.e. the natural system) and how native species are, in turn, affected by these human responses. The key consideration in the source CHANS is whether these human-natural couplings can act to mitigate or exacerbate the rate at which the source region's native species are transported to one or more regions as non-natives.

Source region negative feedbacks

Source region negative feedback loops slow the rate of transport of non-native species into one or more recipient regions. The clearest examples of such feedbacks are locally-instituted quotas or harvest bans associated with the trade of live animals or plants. These top-down



Scheme 1.

regulatory measures are a human response to declining native species abundances that can reduce the exportation rate of the source region's native species (e.g. Rabemananjara et al. 2008). These measures reduce the diversity of species transported as non-natives or the propagule pressures associated with any one of these transported species. This feedback would, however, only form a complete loop if these regulations lead to an increase in the abundance or overall biodiversity of species native to the source region. If so, an additional strengthening of regulations or the adoption of new ones may follow (e.g. building 'legitimacy' in resource management; Pinkerton and John 2008), which may further slow the rate of organism collection and transport. A similar negative feedback loop can occur via bottom-up community interventions to conserve biodiversity by reducing unsustainable or illegal native species collection practices (Cooney et al. 2017). For example, by voluntarily reducing trade to protect a source region's biodiversity or to ensure sustainable trade, the number of species transported as non-natives out of a source location will slow and successful programmes could lead to the refinement or adoption of further interventions.

Negative feedback loops may also arise when people or agencies in the source region become more aware that their native species are considered invasive elsewhere. In this instance, people in the source region respond of their own volition by reducing the intentional or unintentional transport of known invaders. If the impacts of invasion are well-understood or economic incentives are provided to reduce the collection or accidental transport of known invaders out of the source region, the result could be improved detection and removal of hitchhikers before transport or a shift towards trading less harmful species. Cooperative international trade agreements that seek to reduce the further spread of known-invasive species, such as those contained within the International Plant Protection Convention or the Ballast Water Management Convention, embody this shift in international trade and reduction of hitchhikers. Cooperative international trade agreements encourage member nations to commit to actions that reduce the chances that vectors that emanate from their country transport invasive species to others (Keller and Perrings 2011). In this context, a negative feedback loop can result if the removal programmes or types of behaviour enacted in the source region succeed in reducing the number or diversity of transported organisms and these successes, in turn, provide information to reinforce or refine future efforts.

Source region positive feedbacks

Positive feedback source loops result in a continual increase in the quantity or diversity of species native to the source region being transported as non-natives to recipient regions. For example, similar in practice to 'fishing down the food web' (Pauly et al. 1998), if people in the source region respond to declines in their native species by continually shifting the base of exploitation to supply the live-animal or plant trade with the next most abundant or easily accessed species (Harfoot et al. 2018), then their actions ensure a continual increase in the pool of native species transported to recipient regions as non-natives. The same type of feedback loop can result from regulations in the source region that inhibit the collection or use of their declining native species if it drives com-

mercial diversification towards the exploitation of new native species (e.g. Schroth and Ruf 2014). The loop continues if the abundances of newly-exploited species also decline, requiring new protective regulations which could again shift trade towards new species.

With the creation or continuation of a positive feedback loop for species that are intentionally transported, the resulting diversification in the native species transported from a source region will also diversify the transport of hitchhiking organisms associated with these species (e.g. the increasing diversity of zoonotic diseases as the global wildlife trade expands; Chomel et al. 2007). Beyond this example, however, it seems unlikely that positive feedback loops could arise for unintentionally collected organisms, such as plant seeds on clothing or arthropods within wooden pallets. Such feedbacks seem implausible given that people in the source region would have to purposefully increase their ability or propensity to collect and transport such species unintentionally based on changes in local biodiversity.

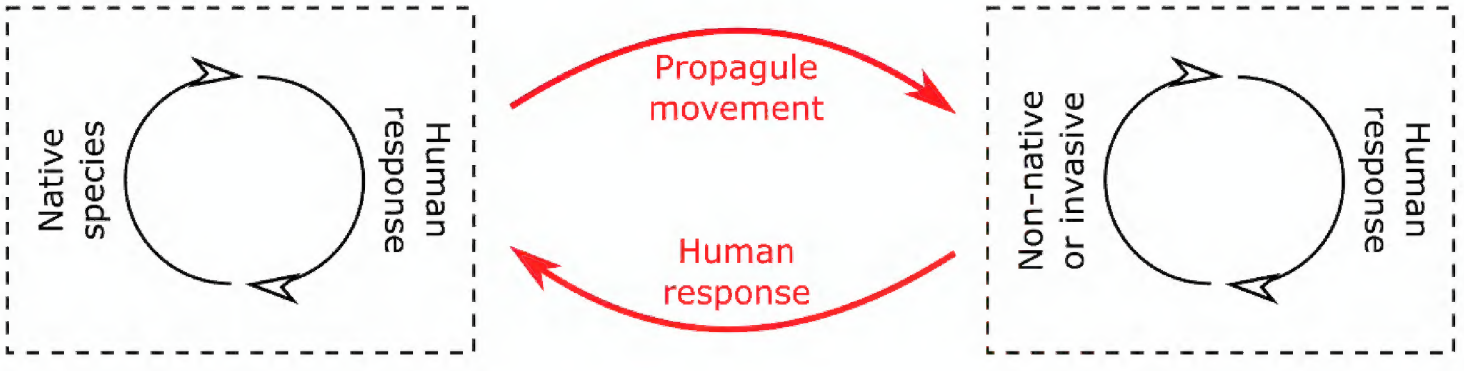
Transport coupling

Drivers of transport feedback loops

There is a well-established association between trade and travel intensity from source to recipient regions and the rate at which non-native species accumulate within recipient regions (Perrings et al. 2005; Hulme 2009; Seebens et al. 2017; Pyšek et al. 2020). A feedback loop can arise in this context if the effects of non-native species in the recipient region drive changes in policy, economics or human behaviour so that trade and travel from the source region either decreases (negative loop) or increases (positive loop). These feedbacks result in a concomitant reduction or acceleration of non-native introduction diversity or rates to the recipient region.

Transport negative feedbacks

Negative transport feedback loops occur when the economic, ecological or cultural costs of invasions in the recipient region incite a human response that reduces the diversity or quantity of species transported out of the source region. A full feedback loop results when this response is then adapted based on how effectively it prevented further



Scheme 2.

invasions or invader effects. For example, the damage caused by multiple invasive species in New Zealand led to government adoption of strict biosecurity measures that limit the importation of novel non-native species from a variety of source regions (Jay et al. 2003). These measures, in turn, prompted industry and government agencies in source regions to impose or strengthen their own pre- or within-transport biosecurity measures, such as adoption of cargo or ballast treatment, so that their products can successfully pass border inspections. The feedback loop was completed when these regulations or incentives were further revised, depending upon whether non-native establishment and spread declined or when a new invader arose (Hayden and Whyte 2003).

Economic feedbacks from the recipient region could also affect non-native species transport if the damage caused by an invader shifts investments towards funding prevention methods that reduce the quantity or diversity of propagules that enter, survive or exit transport vectors (Lodge et al. 2009; Latombe et al. 2020). This feedback loop hinges on the relative costs and benefits of investing in measures that prevent initial introduction compared to focusing on control of already established non-natives or even not managing the invasion process at all. Biosecurity preventative measures could be favoured if, for instance, the costs of pre-introduction treatments are low (Hyytiäinen et al. 2013), the projected or known damage of an invader is high (Marbuah et al. 2014) and if policy-makers are willing to accept the uncertainties of preventing potential invaders over controlling known invaders (Finnoff et al. 2007). There is also a clear potential for a shift in the strength of this negative feedback loop over time. Prevention can be favoured if damage increases as an invasive species' population increases or could be disfavoured if the invasive population declines. New technologies or refined risk assessments (e.g. Kumschick et al. 2020) could also alter the perceived costs versus benefits of investing in preventing non-native transport.

Awareness campaigns or stigmatising trade in particular species (Fischer 2004) provides an alternative type of cultural negative feedback loop that can reduce demand for live species or products that commonly result in the establishment of non-native species in the recipient region. Consumer preferences in the recipient region are a key driver of both intentional trade and unintentional transport of non-native species (Sinclair et al. 2020). Campaigns that target consumers of goods associated with high rates of species invasion can therefore reduce the diversity or volume of species transported from a source region, such as by altering preferences to favour native or non-invasive species (e.g. Drew et al. 2010; Patoka et al. 2018) or by encouraging the use of more sustainable or locally-sourced goods (e.g. Barlow et al. 2014). However, it is unclear whether changes in consumer demand can, in turn, be affected by elevated rates in the introduction and establishment of non-native species, thus completing the full feedback loop. Such a feedback loop might occur if consumer demand continues to decline in response to the success of awareness programmes at controlling non-native introduction rates.

Transport positive feedbacks

Non-native species introductions and subsequent invasion impacts in a recipient region can drive socioeconomic- or policy-based feedback loops that continually increase

non-native species transport out of source regions over time. Increasing introductions of non-native pets and horticultural plants, for example (Mack 2003; Lockwood et al. 2019), has served to increase consumer demand for such products. This increased demand has subsequently elevated trade volume and diversified the number of species within these trades (e.g. Drew et al. 2010; Seebens et al. 2017; Scheffers et al. 2019), creating a potential feedback loop. A similar feedback could result from biocontrol introductions in which the human response to the effects of a non-native species is to introduce another non-native, natural enemy, which could subsequently become invasive and require further control (Simberloff and Stiling 1996). Culturally-driven import and release of traditional live food plants and animals by human communities (e.g. snakehead fish; Cagauan 2007) could also create a positive feedback loop in which the initial successful introduction of desired non-native species to re-create a cultural 'sense of place' can increase the appeal of further introductions (Brook 2003). All of these examples of potential positive feedback loops can produce a socioeconomic version of invasional meltdown (invasive species facilitating further invasions; Simberloff and Von Holle 1999), whereby the human response to non-native species introductions or the effects of these introductions is to desire that more non-native species be introduced, which could in turn spur further introductions (Fig. 3).

Regulation can also create positive feedback loops if the response of the people living in a source region to a policy change enacted in the recipient region is avoidance, rather than compliance. Avoidance behaviour can expand transport into new regions, subsequently increasing the spatial dispersion of transport vectors and thus associated introductions of non-native species. An agent-based model by Ameden et al. (2009) provides an example of such avoidance by showing that importers might respond to increases in invasive species border inspections with 'port-shopping' behaviour by seeking out ports with lower inspection standards. Non-native species blacklists can similarly drive avoidance responses by shifting transport towards as-yet unlisted taxa, subsequently increasing the probability of introducing new non-native species in recipient locations (García-de-Lomas and Vilà 2015). There are also examples in which travel fees in recipient regions can alter human movements rather than prevent or control them (e.g. Chivers et al. 2017) and this same principle could apply to transport vectors travelling between source and recipient regions. A full positive feedback loop can then arise when regulatory efforts subsequently expand to encompass the new regions into which vectors are now travelling, creating an 'arms race' between regulatory policy and avoidance responses.

Recipient region coupling

Drivers of recipient feedback loops

Once non-native species establish within a recipient region, the population abundance or geographical distribution of these species can be reduced or augmented via our final CHANS feedback loop. Here, reciprocal loops are generated by the cultures within a

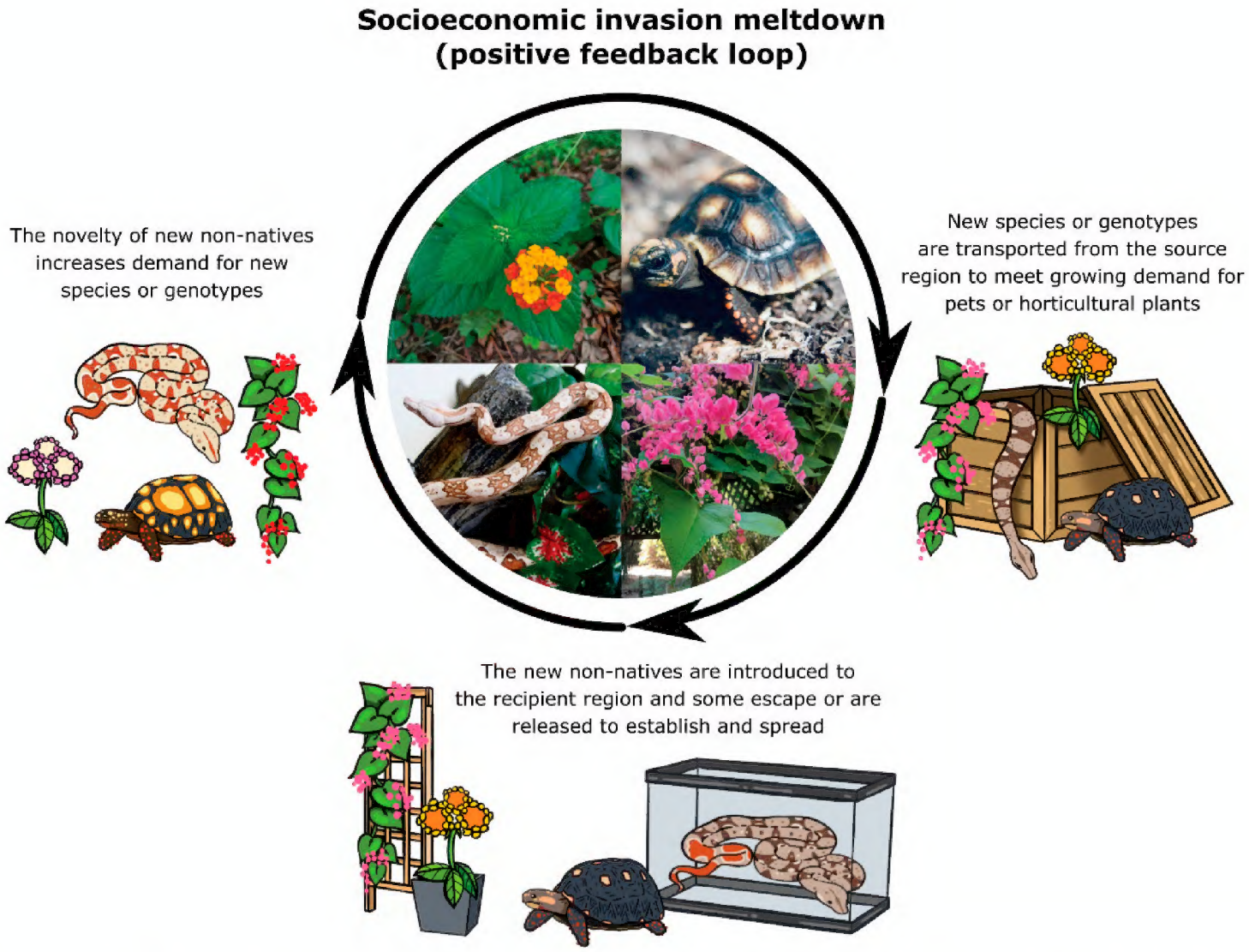
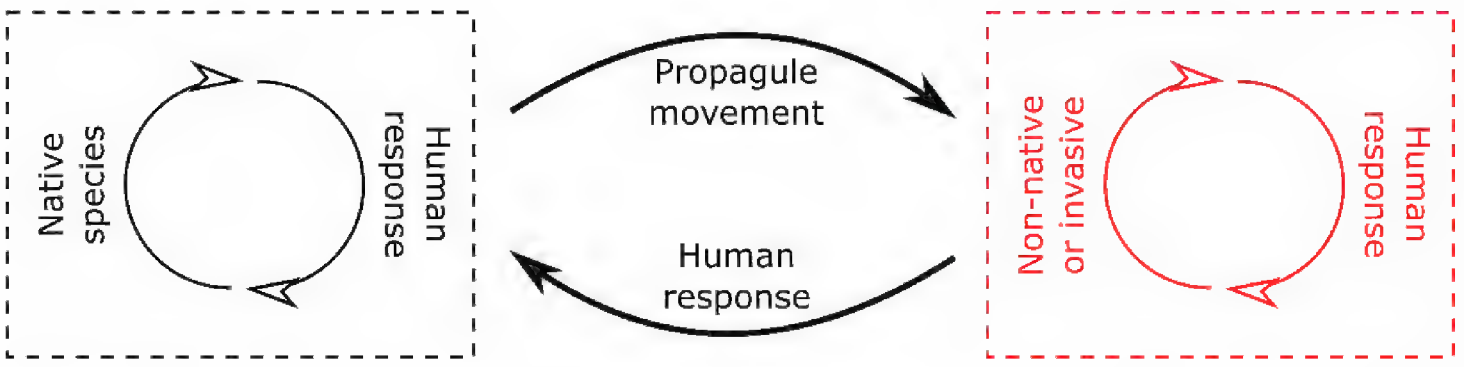

Socioeconomic invasion meltdown
(positive feedback loop)
The novelty of new non-natives increases demand for new species or genotypes
New species or genotypes are transported from the source region to meet growing demand for pets or horticultural plants
The new non-natives are introduced to the recipient region and some escape or are released to establish and spread

Figure 3. A conceptualisation of an invasion positive feedback loop driven by intentional introductions of non-native species for the horticulture or pet trades. The example species used are, from the top left of the centre photograph and moving clockwise, Lantana (*Lantana camara*), the red-footed tortoise (*Chelonoidis carbonarius*), coral vine (*Antigonon leptopus*) and the red-tailed boa (*Boa constrictor*). Each species has a history of intentional introduction and successful establishment in recipient regions. Drawings with different colours are based on actual colour varieties or morphs of these species. The plant photographs were provided by James Sinclair (the first author), the animal photographs were provided by Keara Clancy (Department of Wildlife Ecology and Conservation at the University of Florida) and the drawings were commissioned from Marie-Josée Létourneau for use in this manuscript.

recipient region and the perceptions of risks and benefits that established non-native species present (Trigger 2008; Gaertner et al. 2017; Vimercati et al. 2017; Polák et al. 2019; Potgeiter and Cadotte 2020). These perceptions will feed back towards either inhibiting or accelerating the population growth rate, geographical range expansion and/or secondary spread of established non-native species and, thus, their impacts which, in turn, will affect how the non-native is perceived (Shackleton et al. 2019).

Recipient region negative feedbacks

Non-native species that cause ecological or economic damage or that disrupt cultural and recreational activities can instigate a negative feedback loop via instigating control or eradication efforts or incentivising the use of native species or products that do not



Scheme 3.

facilitate secondary spread of non-native species. A full negative feedback loop occurs if self-, community- or government-enforced initiatives against harmful non-native species successfully limits their abundance or distribution or promotes awareness that facilitates management and reduces further spread (e.g. Klapwijk et al. 2016). These successes are then used to refine or inspire future efforts (e.g. Simberloff 2009). In this way, the human system is continually responding to ongoing changes in the natural system to better balance or mitigate invasions. An example of this feedback loop is when invasive trees or grasses restrict homeowner site lines or invasive aquatic plants limit boating and fishing opportunities and individual homeowners respond by actively reducing the population abundance of the non-native on their property (Charles and Dukes 2007; Niemiec et al. 2017). Invasive species can also pose risks to the persistence of culturally-valuable native species, such as the risk that the invasive emerald ash borer will result in the near-total loss of native ash trees that feature in the origin of stories about Native American tribes (Poland et al. 2017). When such damage to cultural or aesthetic amenities occurs, there is often a strong desire by residents to restore a 'natural' aesthetic by managing the invasive species or imposing stricter regulation of invasive and non-native species use or related goods (Dickie et al. 2014; Kueffer and Kull 2017). These individual responses can create full feedback loops when communities organise to form self-promoting groups to control several non-native species. Often membership in these groups or the social acknowledgement people receive from these groups, leads to more individuals joining, thus creating a social expectation of further engagement in non-native species management (Niemiec et al. 2016). This feedback can be reinforced when community groups exert considerable pressure on local governments to initiate management actions, which often happens due to local media attention or when the communities feel the potential threat of a growing invasion (Crowley et al. 2017).

Recipient region positive feedbacks

Many non-native species can elicit sympathetic reactions from people who have a historical relationship with these taxa or who are not aware of the issues presented by invasive species. Non-natives can also become more positively perceived through time as people may view pest species positively or novel if population sizes decline (Shackleton et al. 2019) and fear

of non-natives can decrease with increased familiarity to the damage they can cause (Schüttler et al. 2011). Sympathetic or positive reactions to established non-native species can drive their increased population growth rates or enhanced dispersal potential via the human desire for their further establishment and spread. These actions can, in turn, expose new people to the non-native species and reinforce secondary spread through positive associations with the non-native, creating a positive feedback loop. For example, people in many regions have intentionally introduced non-native species for aesthetic or cultural purposes and, in some cases, these species have become culturally significant, resulting in a cultural desire for continued population growth or range expansion of the non-native species (Nuñez and Simberloff 2005). Due to this connection, non-native species that may be economically detrimental, but elicit sympathy through the human-animal bond (e.g. deer) or have charismatic features, such as song or colouration, may enjoy little to no reductions in their individual survival or reproduction rates due to push-back from citizens to proposed control measures (e.g. common lionfish; Jimenez et al. 2017). In fact, for many such species, people will actively promote survival and spread rates of non-natives through supplemental feeding and other protection (Robinson et al. 2005; Bonter et al. 2010). Even with invasive species, particularly horticulture plants introduced for aesthetics that have significant ecological impacts but limited negative or positive economic impacts (e.g. bamboo and tallow tree), invasive populations may be spread prolifically through continued local transport and intentional planting or release. This feedback occurs because, as populations of these invasive species spread, more people encounter the species which, in turn, fosters the desire for people to further the species' spread via intentional planting (e.g. Bradley et al. 2010).

Positive feedback loops can also occur when an invader becomes integrated with human communities in the recipient region as a resource (Robinson et al. 2005; dos Santos et al. 2014; Vilá and Hulme 2017), subsequently leading to human actions that promote further spread or that oppose control or eradication efforts. Many non-native species, for instance, have become key targets for hunting or provide essential food sources for local communities (Jean Desbiez et al. 2011). In several such circumstances, traditionally-hunted native species have declined as a result of past over-exploitation or the ecological impacts of other invasive species, resulting in a cultural shift in hunting practices towards exploitation of a non-native (Robinson et al. 2005; Jean Desbiez et al. 2011). Over time, responding to ongoing declines in native species by continually spreading a non-native, may become the cultural norm and the perception of the new species as 'non-native' may be lost (Semenya et al. 2012; Shackleton et al. 2015). People may also facilitate the secondary spread of established and valuable non-natives to new areas in response to its growing value as a resource (Nuñez et al. 2012), creating a full feedback loop.

Lastly, management responses to non-natives that do not account for human behaviour could drive positive feedback loops through an arms race between regulation and non-compliance. These types of feedbacks are more thoroughly discussed in the source and transport CHANS sections above, so we will not delve into them too deeply again, but it is important to acknowledge their localised role in the recipient region. Examples of potential positive feedbacks include access or cleaning fees levied to reduce unintentional non-native spread, which can instead drive the secondary spread of non-natives into new locations (Chivers et al. 2017). Similarly, localised restrictions on the sale or purchase of non-native

species can drive customers to seek out nearby, unregulated vendors (e.g. shifting the within-state US trade of horticultural plants to out-of-state sources; Maki and Galatowitsch 2004). Efforts aimed at collecting non-natives from the broader public, such as pet or plant surrender programmes, could also perversely cause non-native species releases if people do not perceive participation to be personally cost effective or convenient (Drake et al. 2015). These examples can become fully realised positive feedback loops if the result of the human response is an increase in non-native species establishment, spread or impacts which, in turn, drives the adoption of further management responses that are again avoided.

Implications for Invasion Science

There is extensive literature on human responses to non-native and invasive species, but rarely are feedback loops within or across invasion stages explicitly considered (cf. Lodge et al. 2009; Howard 2019; and Hulme et al. 2020 for parallels with epidemiology). The recognition that three distinct CHANS can occur across the invasion process and that each can create negative and positive feedback loops, provides three key insights to invasion science.

Firstly, a CHANS perspective highlights that recipient region invasions are inextricably linked to interactions with the source region and that human-nature feedbacks, localised solely within the source, can drive invasion dynamics. This is a key insight because many invasion frameworks overlook processes that occur prior to non-native species introduction as potential drivers of accelerating global invasion rates (Sinclair et al. 2020). Considering how policy, economic and cultural feedback loops within the source region subsequently affect the invasion process and human-nature interactions in the recipient region could therefore be crucial for predicting how introductions may change in the future and for improving invader management (i.e. the same implications of a better focus on the 'supply-side' of invasions discussed by Verling et al. 2005).

Secondly, the continual feedback between people and native or non-native species in the CHANS we have outlined could produce unexpected or unpredictable interactions that may continue to change over time as humans respond and adapt to the presence of non-native species. These types of emergent effects are discussed more fully in other literature (e.g. CHANS or social-ecological systems; Liu et al. 2007; Preiser et al. 2018) and include: (i) legacy or lagged responses; (ii) thresholds and resiliency between alternate states; and (iii) indirect effects. Though not discussed from a CHANS perspective, there is evidence that these types of interactions can manifest in the invasion process. Examples include current invasions that are a legacy of past human-nature interactions (Essl et al. 2011), introductions that drive regime shifts in how people interact with non-native species (Shackleton et al. 2018), and indirect human responses to non-natives of changing demand for goods or services rather than direct control of local populations (Drew et al. 2010). This potential for complex and surprising human-nature interactions in invasions highlights a need to re-examine (and potentially revise) current hypotheses about the major drivers of invasion rates to address how humans might be shaping the ecological processes involved. Efforts to understand invasions that lack a consideration of human components will in-

crease the likelihood that surprising, interactive effects will arise (Pyšek et al. 2020) and interventions, based on such incomplete knowledge, could generate new problems or even exacerbate invasions (e.g. control policies that drive a positive feedback loop).

Thirdly and finally, the potential existence of the three CHANS we have outlined highlights that there is still a great deal we do not know about how people and non-native species interact. Many of the example feedback loops we reviewed are theorised, simplified representations of complex interactions. We have supported our ideas where we can with background literature, but there is simply not enough research to fully specify the complete feedback loop for any one example. Further work is thus required to confirm that these CHANS exist as we have outlined and, if so, to fill in the complexities within each. Examples of such complexities include potential variability in the strength and relevance of each CHANS amongst different types of intentional and unintentional invasion pathways (e.g. intentionally released versus escaped non-natives; Hulme 2009). Feedback relevance may also shift across stages of the invasion process, such as accidental escapees or hitchhikers that are initially affected by policy or economic feedbacks, but cultural feedbacks may become more relevant as people become aware of the invader's impacts in the recipient environment. The prevalence of the non-native species-to-people portion of invasion feedback loops is also potentially complex. Examples of one-way feedbacks in which people respond to non-native species abound in the invasion literature (e.g. intentional introductions to encourage establishment or eradication programmes to remove spreading invaders), but less is known about how readily this human response is affected by subsequent changes in the non-native species themselves (but see examples in Howard 2019). Therefore, while our approach serves to deepen continuing efforts in invasion science and ecology as a whole to better account for the role of humans in natural processes, we have only scratched the surface of the milieu of potential interactions that likely exist between people and non-native species.

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